

LATE TERTIARY RADIATION OF VIPERFISHES (CHAULIODONTIDAE) BASED ON A COMPARISON OF RECENT AND MIOCENE SPECIES.

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ABSTRACT: The Miocene species *Chauliodus eximius* from southern California is redescribed and compared with all extant species of the genus. Postponement of the time of ossification of the anterior vertebrae in some recent species is considered as the major speciating mechanism in the late Tertiary. *Chauliodus sloani* is proposed as the first modern species to possess this characteristic. Patterns of radiation from the eastern Pacific are suggested to explain the present geographical distribution of the family.

INTRODUCTION

The family Chauliodontidae is represented by the single genus *Chauliodus*. Berg (1947) places this family in the order Clupeiformes (Isospondylii), suborder Stomiatoidei, superfamily Stomatoidae (Lepidophotodermi). Gossline (1960), in his revision of Clupeiformes, concurred but added the division Clupei. Greenwood, *et al.* (1966) suggests that the suborder Stomiatoidei be placed in the order Salmoniformes, superorder Protacanthopterygii, Division III. Six species are recognized in the latest revision of the genus by Morrow (1961) with representatives found in the temperate and tropical regions of all oceans. These species occur at depths ranging from 20 to 2,800 meters with the greater depths characterized by larger specimens. There appears to be a segregation of distinct populations in different water masses (Haffner, 1952). This has resulted in the description of a number of species and subspecies.

The first description of the genus was by Catesby (1771) who assigned the name *Vipera marina*. His designation was invalidated by opinion no. 89 of the Commission for International Rules of Zoological Nomenclature which eliminated all the systematic names devised by Catesby. The first recognized use of the name *Chauliodus* was by Bloch and Schneider (1801) in describing *C. sloani*.

The remaining living nominal species and subspecies were described in the following order: *Chauliodus macouni* Bean (1890), *C. pammelas* Alcock (1892), *C. barbatus* Garman (1899), *C. dannevegi* McCulloch (1916), *C. danae* Regan and Trewavas (1929), *C. sloani secundus* Ege (1948), *C. sloani schmidtii* Ege (1948). In 1961, Morrow placed *Chauliodus dannevegi* and *C. sloani secundus* in synonymy with *C. sloani* and elevated *Chauliodus sloani schmidtii* to specific rank.

Jordan and Gilbert (in Jordan, 1925) described a fossil specimen from Lompoc, California as *Eostomias eximius*. In 1943, David recognized the specimen as a viperfish and changed the name to *Chauliodus eximius*. The type

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specimen has been declared lost, according to Dr. George S. Myers, Division of Systematic Biology, Stanford University, after a thorough search by the author.

Chauliodus barbatus frazeri David (1943) was described on the basis of one almost complete specimen and several fragments from the upper Modelo formation (upper Miocene) of the Santa Monica Mountains, Los Angeles County, California. A search of the literature and personal communication with Prof. Camille Arambourg, Musée Nationale d'Histoire Naturelle, Paris, France, indicates that no other fossil specimens of the genus were known prior to 1959 despite the fact that fossil faunal assemblages similar in their deep sea aspects to those in southern California have been reported from the late Miocene of North Africa and Italy, and the Oligocene of the Carpathian Mountains and of the Caucasus (Arambourg, 1927; Jerzemska, 1960; Danilchenko, 1960). Since then, 43 additional fossil specimens of *Chauliodus* have been collected in southern California. This new and more complete fossil record forms the comparative basis for this paper.

METHODS AND MATERIALS

I. Recent forms

Alcohol-preserved specimens of *Chauliodus barbatus* (17 specimens), *C. macouni* (35 specimens), *C. sloani* (23 specimens), *C. danae* (14 specimens), *C. pammelas* (12 specimens), and *C. schmidtii* (3 specimens) were X-rayed or cleared and stained using the Hollister (1934) technique.

Satisfactory radiographs were obtained by using Kodak Industrial type M film with two types of Soft X-ray units, G.E. Mobile 90-11, and Softex "B", KKK, Tokyo. A hospital unit, Picker "300," was unsatisfactory using Dupont SL-313 and Kodak Blue Brand films because even the lowest voltage overexposed the negative and the film was too grainy for good definition. Since the outlines of alcohol drops show on the film, the specimens were first blotted dry, then positioned on a thin sheet of clear plastic laid over the loaded cassette. Varying degrees of exposure on a single specimen were achieved either by blocking out an area by building a bridge with a lead sheet or laying several thicknesses of paper toweling over the tail or other portions likely to be burned out by overexposure. The latter method was very effective and time-saving since it eliminated the necessity for two separate exposures. Test film was exposed to determine the optimum exposure for each size range. The results are summarized in Table 1.

The fossil specimens were X-rayed, but the results were unsatisfactory. Some barely visible outlines were obtained with the Softex "B" machine at 6 MA, 15 KV, 10 inches, with a two minute exposure. Further experimentation in this area should prove fruitful.

Measurements and counts were made from the X-rayed or stained material of those characters which may be discerned in these fossils. Such

TABLE 1
*X-ray data for the genus Chauliodus using
 Kodak Industrial Type M film*

X-ray Model	Standard Length (mm.)	Milli- amperes	Kilo- volts	Exposure Time (sec.)	Distance (inches)
G.E. Mobile 90-II	50	5	40	20	40
	175	5	40	50	40
KXX Softex-B	50	6	15	3.5	10
	80	6	15	5	10
	125	6	15	15	10
	125	6	15	35	16
	190	6	15	30	10

characters include the teeth, vertebral column, fins, and general body proportions but exclude otoliths, scales, and most of the bones of the head. Photophores of the ventral series appear in only two fossil specimens. In addition to the generally accepted meristic and morphometric characters used in fishes, the following counts and measurements were used:

1. *Number of cervical vertebrae*: Counted from the second vertebra and specifically excluding the most anterior vertebra (which possesses an enlarged neural arch, no centrum, and an enlarged haemal arch) to that vertebra on a vertical line drawn from the base of the first dorsal ray. (Note: All vertical and perpendicular lines are drawn in reference to the axis of the vertebral column.)

2. *Number of acenous vertebrae*: Counted from the second cervical vertebra, specifically excluding the first cervical vertebra, which is not discernible in the fossil because it is obscured by the supracleithrum and is therefore omitted from all counts. Only those vertebrae without any trace of ossification of the centrum were included in this category.

3. *Number of thoraco-abdominal vertebrae*: Counted from, but not including, the last cervical vertebra to that vertebra on a perpendicular line from the first anal ray.

4. *Number of caudal vertebrae*: Counted from the last thoraco-abdominal vertebra.

5. *Number of vertebrae under dorsal fin*: Counted between vertical lines drawn from the base of the first dorsal ray and the base of the last dorsal ray.

6. *Number of vertebrae over pelvic bone*: Counted between perpendiculars drawn from the anterior-most margin of the pelvic bone and from its articulating border.

7. *Number of vertebrae over anal fin*: Number of vertebrae between perpendiculars drawn from the base of the first anal ray and from the base of the last anal ray.

8. *Length of head*: Distance between vertical lines from the anterior tip of the premaxillary and to the most posterior margin of the cleithrum.

9. *Length of caudal peduncle*: Measured from a vertical drawn from the base of the last anal ray to the end of the hypural.

10. *Length of teeth*: Measured as the distance in a straight line between the tip of the tooth and its point of emergence from the bone. No attempt was made to follow the curvature of the tooth.

11. *Standard length*: Measured from the anterior margin of the premaxillary to the posterior margin of the hypural.

A few of the fishes examined were so damaged by capture, preservation, or preparation methods that data from them are incomplete. However, usable data from these specimens were retained.

II. Fossil forms

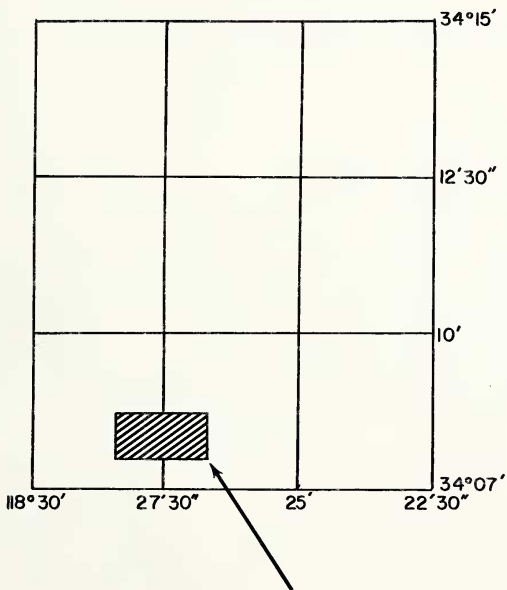
The holotype of *Chauliodus barbatus frazeri* David, from California Institute of Technology (CIT) Location No. 326 (Fig. 1) was cleaned and examined, as were two fragments from CIT 385. Forty-three additional specimens from Los Angeles County Museum of Natural History (LACM) Locations Nos. 1035, 1267, 1806, 1925, 6589 and CIT 332 were collected and measured in the manner previously described. Six of these specimens are complete. Parts of the remaining specimens were either lost in collecting, broken in preparation, or had been lost prior to fossilization. In some, the bones of the head were disarticulated. It was necessary in preparing the teeth to destroy some of the bones in the area of the mouth. If bones were scattered or fragmented, only those components which could be measured accurately were used. The supracleithrum generally obscured the area of the centrum of the anterior-most vertebrae. No attempt was made to remove this bone.

Thirty of the specimens collected came from LACM No. 1267 (Fig. 1) at the northeast end of the Santa Monica Mountains, Los Angeles County, California, in the most easterly portion of what is now an inaccessible San Diego Freeway (Interstate Highway 405) road cut. The remaining specimens were unearthed at LACM No. 1806: Milbrook Road, Beverly Glen Canyon, Santa Monica Mountains (Fig. 1); LACM No. 6589: Brush Ridge Quarry, near Lompoc, California; LACM No. 1925: Cabrillo Beach, San Pedro, California; LACM No. 1035: behind Mulholland Fire Station, Santa Monica Mountains, Los Angeles County, California; CIT 332: Sulfur Canyon, Santa Susana Mountains, Ventura County, California; CIT No. 385: near LACM 6589, Lompoc, California.

The fact that *Chauliodus* is a relatively small fish made it possible to collect good materials using small hand tools. All of the fossils were found by splitting the diatomaceous shale in the field and then finishing the cleaning in the laboratory. Rocks were trimmed with a handsaw to facilitate transportation and storage. In no instance was any portion of a fossil lost or damaged because of this technique. The greatest damage was done as the rock was split initially, when a pick or chisel inadvertently went through part of an unseen specimen.



Figure 1. Map of a portion of the Santa Monica Mountains, Los Angeles County, California, showing collecting localities of *Chauliodus eximius*, LACM Nos. 1267, 1806, CIT No. 326.



Location of map in Van Nuys Quadrangle U.S.G.S. 1953.



Figure 2. Photograph of *Chauliodus eximius*, LACM Specimen No. 5244, showing photophores and typical body form. Anterior vertebrae are displaced laterally.

The fossils are thin, brittle, compressed remains, appearing brown when laminated between the sheets of punky white diatomaceous rock in which they are found. Frequently portions of the skin are present as an ultra-thin film readily destroyed by contact. Two specimens show carbonized spots representing photophores (Fig. 2). Because of the delicate nature of this material, cleaning was done under a dissecting microscope using needles with flattened points and modified dental cleaning tools. The cleaned surface was sprayed lightly with clear Krylon plastic spray to protect it from abrasion. Saturating the rock with the plastic resulted in a contraction of the saturated area as the plastic hardened, causing that portion of the rock to lift off the plane beneath it. This was a desirable cleaning technique for removing overlying matrix. When too much plastic was applied to fossils lying in thinly bedded diatomite, it caused the fossil to lift off in a thin, brittle sheet.

In order to establish a basis for comparison between extant forms which have been extensively described (Morrow, 1961; Ege, 1948) and the fossil species whose description was based on a single, now lost, specimen (Jordan, 1925) or on an incomplete specimen (David, 1943), it is necessary to re-

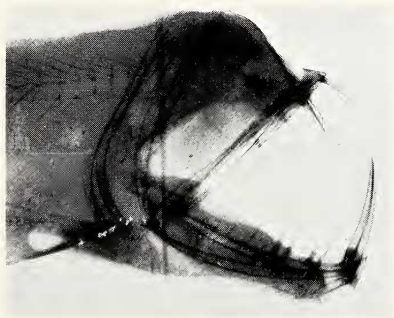
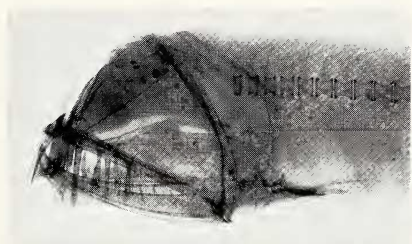


Figure 3. X-ray photograph of adult specimen of *Chauliodus macouni*, showing the single acenous cervical vertebra at the anterior most end of the vertebral column.

Figure 4. X-ray photograph of adult specimen of *C. barbatus* showing single acenous cervical vertebra and partial ossification in vertebra immediately posterior.

Figure 5. X-ray photograph of adult specimen of *C. danae* showing five acenous cervical vertebrae.



Figure 6. *Chauliiodus eximius*, juvenile, 68 mm. SL, LACM specimen No. 11,440, showing greatest ossification in caudal region.



Figure 7. Enlargement of cervical region of Figure 6.



Figure 8. *Chauliiodus eximius*, adult, approx. 160 mm. SL, LACM specimen No. 11,441, showing apparent complete anterior ossification.

describe the fossil in terms comparable with modern data. For this purpose, the David specimen is inadequate and the following description is therefore based on the additional fossil specimens collected since 1959.

RESULTS

Acentrous vertebrae: Examination of X-rays of up to 67-mm. standard length juvenile specimens of all extant species of *Chauliodus* reveals that ossification of the vertebral column begins in the caudal region and proceeds anteriorly as the size of the organism increases. In *C. barbatus* and *C. macouni* the number of acentrous vertebrae continues to decrease until a minimum of one is reached at a standard length of about 145 mm. in *C. macouni* (Fig. 3) and about 178 mm. in *C. barbatus* (Fig. 4). In the remaining extant species, ossification of vertebral centra appears to cease at the fifth, sixth, or seventh vertebra. One unusually large specimen (272 mm.) of *C. sloani* showed 2, possibly 3 (specimen badly distorted in this area), acentrous vertebrae. *Chauliodus danae* is used in Figure 5 as an example of a species with five acentrous vertebrae.

In an exceptionally well preserved fossil specimen of a juvenile *Chauliodus eximus* 68 mm. in standard length (LACM specimen No. 11,440), ossification is shown to be greatest in the caudal region and progressively less as it proceeds anteriorly (Fig. 6). The area of acentrous vertebrae (Fig. 7) is the greatest of any of the fossil specimens. In larger specimens, 86 to 161 mm. in standard length, ossification has proceeded to the point where there are 0-2 acentrous vertebrae evident (Fig. 8). A comparison of the fossil and Recent species with regard to acentrous vertebrae is shown graphically in Fig. 9.

Vertebral counts: A summary of cervical, thoracic and caudal counts for all known species of *Chauliodus* appears in Table 2. The proportions of vertebrae over the pelvic bone, over the anal base, and under the dorsal base for adult *C. macouni*, *C. barbatus*, and the fossil *C. eximus* within the same size range are shown in Figure 10.

Dentition: The general arrangement and size of the teeth in the fossil specimens are typical of the family Chauliodontidae. Measurements of teeth made of intact premaxillary and mandibular teeth in *C. eximus* (Specimen Nos. LACM 5244, 5247, 5248, 5250, 5253, 5254, 5256, 5258, 5260, 5261; LACM: CIT No. 10163; 2 uncatalogued) showed that in twelve out of thirteen specimens in which comparison of the third and fourth premaxillary tooth was possible, the third was longer than the fourth. In specimen No. LACM 5253, the two were equal in length. No measurements were made on the modern species because the data are reported in the literature by Morrow (1961: 253). *Chauliodus macouni* and *C. barbatus* are the only living species having the third premaxillary tooth longer or rarely equal to the fourth.

In *C. eximus* the first mandibular, and the second and third premaxillary teeth show no terminal modification into a triangular expansion generally

typical of *C. sloani*, *C. danae*, *C. pammelas* and *C. schmidtii*. Both *C. barbatus* and *C. macouni* show only a slight terminal modification of these teeth. There is no recurving of the teeth in *C. eximius* as is found moderately developed in *C. macouni* and *C. barbatus* and distinctly in all other species of this genus.

Fin rays: The dorsal fin in all living species has a minute first fin ray followed by an elongated filamentous second ray plus five, rarely four or six, smaller rays. Morrow (1961: 262) describes the first ray as much produced into a long filament, thereby omitting mention of the minute first true dorsal ray. *Chauliodus eximius* seems to possess the minute first dorsal ray. It is difficult to determine the presence of this first ray with certainty because of its small size, proximity to the base of the filamentous second ray, and the general state of preservation. The total dorsal ray count for *C. eximius* including the presumed minute first ray is seven to eight.

Counts of the rays in the paired fins of the fossil specimens were difficult to make accurately because the rays had split during the process of fossilization. Estimates of the pectoral and ventral fin rays place *C. eximius* within the range of the genus. The anal fin in *C. eximius* has 10 to 13 rays which is the same as the range for *C. macouni*, *C. barbatus*, and *C. sloani*. *Chauliodus danae* and *C. schmidtii* have 10 to 12 anal rays and *C. pammelas* has 12 to 13 rays. No counts of caudal fin rays were made.

TABLE 2

Comparison of vertebral counts in Miocene and Recent species of Chauliodus. Brackets surround data from Morrow (1961). N = number of specimens used for each count.

Species	Total	Vertebrae (without first cervical)		
		Cervical	Thoracic	Caudal
<i>eximius</i> (fossil)	48?/50-54 N = 16	9.2(8.5-10) N = 22	32.2(30-35) N = 12	9.8(9-11) N = 13
<i>barbatus</i>	50-54 N = 15	12.6(10.5-14.0) N = 14	29.7(28-32) N = 15	10.3(9.0-11.5) N = 15
<i>macouni</i>	56-60[55-61] N = 29	10.5(8.5-12.5) N = 27	36.8(35-39) N = 29	10.3(10.0-12.0) N = 27
<i>sloani</i>	53-58[61] N = 20	9.2(8-11) N = 19	36.7(33-39) N = 19	9.4(9-10) N = 20
<i>danae</i> (Gulf of Mexico)	53-56[50-56] N = 8	12.6(12-13) N = 8	32.0(30-34) N = 8	9.6(9-10) N = 8
(Peru-Chile Trench)	58-60 N = 6	12.1(12-13) N = 6	35.2(34-36) N = 6	11.6(11-12) N = 6
<i>pammelas</i>	51-53[49-52] N = 10	9.5(9-10) N = 11	32.1(30-33) N = 9	10.2(9-11) N = 9
<i>schmidtii</i>	53[51-54] N = 1	8 N = 1	34 N = 1	11 N = 1

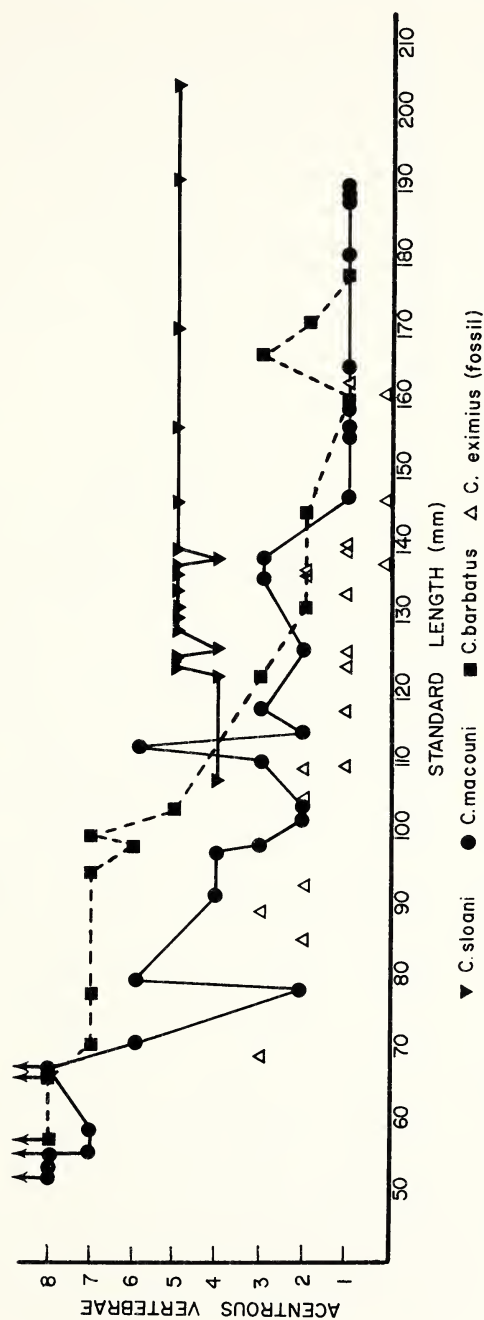


Figure 9. Graph showing relationship between standard length and number of acenitrous vertebrae in three Recent and one fossil species of *Chauliodus*. Arrows indicate that the number of acenitrous vertebrae exceeds eight but an exact count is not possible. *Chauliodus danae*, *C. pammelas*, and *C. schmidti* of comparable size follow a pattern similar to *C. sloani*.

Measurements of length: Measurements from the snout to dorsal origin are shown as an average percentage of the standard length in Figure 11. Snout to anal origin, length of anal base, and the length of the caudal peduncle are similarly represented in Table 3. The snout to dorsal origin shows a steady progression of the dorsal fin posteriorly from the fossil to *Chauliodus barbatus* and *C. danae*. Beginning with *C. macouni* the trend is reversed as the dorsal fin is advanced.

In *C. danae* the anal fin is more posteriorly placed than in any other, and the fin itself is the shortest. In *C. barbatus* the anal fin has advanced somewhat while the size of the fin has remained constant.

In all species the caudal peduncle has increased in length over the fossil form. The greatest increase is in *C. barbatus*.

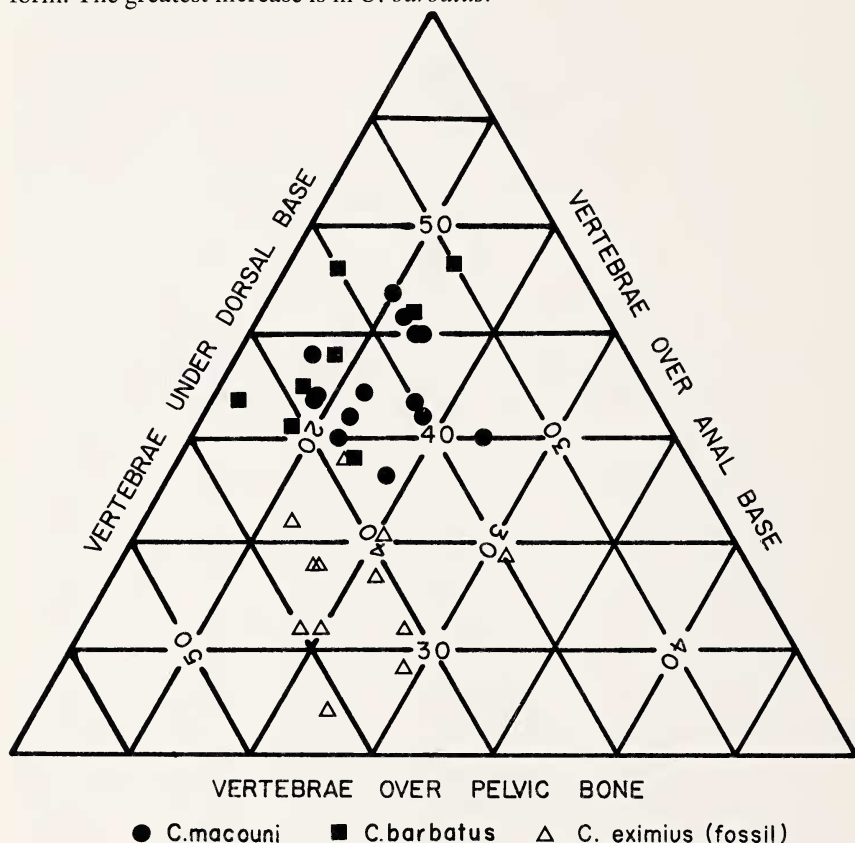


Figure 10. Triangular graph comparing the proportional distribution of vertebrae within individuals of two Recent and the Miocene species of *Chauliodus*. (Each point represents a single fish whose vertebral counts in the areas represented have been summed and each count plotted as a percentage of this sum. The coordinates of any point on this graph, therefore, add up to 100%.)

TABLE 3

Comparison of caudal region of Miocene and modern species of Chauliodus.

All figures expressed as average
percentage of standard length.

Species	Snout-anal origin (data, except fossil, from Morrow, 1960)	Length of anal base	Length of caudal peduncle
<i>danae</i>	86.0	6.6	7.4
<i>barbatus</i>	81.8	8.8	9.4
<i>eximius</i> (fossil)	84.6	8.9	6.5
<i>macouni</i>	83.8	8.1	8.1
<i>pammelas</i>	83.0	9.0	8.0
<i>sloani</i>	84.6	7.5	7.9
<i>schmidtii</i>	84.8	8.2	7.0

DISCUSSION

Acentrous vertebrae: Tchernavin (1953: 23) states, "In *Chauliodus* (as in many Stomiatooids) the anterior part of the notochord, corresponding probably to seven vertebrae, persists through life . . ." Counts of *acentrous vertebrae* from X-rayed and cleared specimens of extant species of *Chauliodus* indicate that this statement is not applicable to *C. barbatus* or *C. macouni*, since the extent of ossification is a function of size in these species (Fig. 9). Examination of juvenile stages of these two species shows that ossification occurs first in the anal region and proceeds anteriorly to the first cervical vertebra which remains unossified throughout the adult life. (For a resume of larval development, see Morrow, 1964.)

In *Chauliodus sloani*, *C. pammelas*, *C. schmidtii* and *C. danae* the anterior 4 to 5 vertebrae remain unossified up to 200 mm. standard length. Specimens of all these species in excess of 200 mm. were not available for examination, but the one *C. sloani* at 272 mm. with only two vertebrae remaining unossified suggests that this may be the ossification pattern for the others as well. Juvenile stages of all species likewise were not available. Seemingly they would show a growth pattern of ossification, up to the fourth or fifth cervical vertebra, similar to that of *C. barbatus* and *C. macouni*.

The low (1 to 2) *acentrous* counts in *Chauliodus eximius* may not be accurate because there may be no *acentrous vertebrae* at all. No specimen clearly shows the complete anterior-most portion of the vertebral column because in all specimens it is obscured by the fragile supracleithrum and dislocated small bones. Since the count of *acentrous vertebrae* in X-rayed individuals of modern species is based on observable paired neural and epineural spines, and since the position of these elements and the spacing of centra in this material indicates that some evidence of the anterior vertebrae should be visible in fossil specimens, it is believed that the estimates of the vertebral number in *C. eximius* are fairly reliable. It is logical to assume that the Miocene

fishes displaying ossification of the vertebrae up to at least the second cervical vertebra, and possibly with all vertebrae ossified, represent a primitive condition and that the increase in the number of anterior acenous vertebrae typical of many living forms of this genus is a subsequent evolutionary modification.

The spacing between the cervical vertebrae in all species of *Chauliodus* is greater than in other portions of the vertebral column. This increases the flexibility in the anterior portion of the body. Increasing the number and decreasing the length of the anterior vertebrae increases flexibility even further. The unossified notochord provides still greater flexibility than either increased spacing or increased numbers. The feeding habits of *Chauliodus* involve very great flexion of the cervical region (Tchernavin, 1953). Seemingly the retention of the acenous condition in the adult has great survival value to *Chauliodus sloani*. This species has a greater geographic distribution than any other species of the family Chauliodontidae, and this is probably due to its more efficient food-catching abilities—the result of the retention of the larval acenous condition in the cervical region.

Similarly, the acenous cervical vertebrae in *Chauliodus danae*, *C. pammelas*, and *C. schmidt* confer a feeding advantage upon these species.

Vertebral counts: Since the method used here of counting cervical, thoracic, and caudal vertebrae is dependent upon the positions of the dorsal

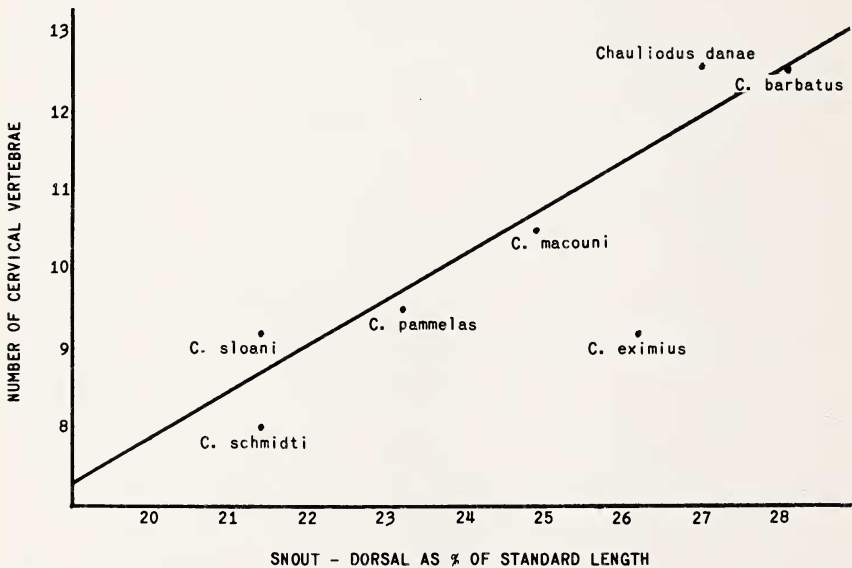


Figure 11. Graph relating the number of cervical vertebrae and the position of the dorsal fin in *Chauliodus* spp. The curve ($y=0.59X-3.94$) represents the "best fit" line derived by the method of least squares.

fin origin and the anal fin origin, it is necessary to compare the various counts with the positions of the referred elements. Thus, in Figure 11, it may be seen that the number of cervical vertebrae has increased by at least one from the fossil to *Chauliodus macouni* and by at least three from the fossil to *C. barbatus*. The remaining apparent differences are the result of the movement of the dorsal fin. The movement of the dorsal fin in *C. macouni* and *C. barbatus* plus the increase in number of cervical vertebrae increased the flexibility of the cervical region giving these two species a feeding advantage over *C. eximius*. In *C. danae* flexibility reaches a maximum when acenous vertebrae are combined with the features of high cervical vertebral count and posterior placement of the dorsal fin.

Chauliodus sloani, *C. pammelas* and *C. schmidt* tend to maintain or reduce the number of cervical vertebrae but achieve flexion by reducing cervical ossification.

The thoracic vertebrae count depends on both the position of the origin of the dorsal fin and the position of the origin of the anal fin. In *Chauliodus barbatus*, the anal fin has moved forward slightly as the dorsal has moved posteriorly resulting in a decrease in thoracic vertebrae. *Chauliodus danae*, whose dorsal fin position relative to *C. barbatus*, is unchanged, and whose anal fin is most posterior, has gained thoracic vertebrae. *Chauliodus macouni* and *C. sloani* whose dorsal fin has moved forward have relatively fixed anal fin origins. Each appears to have gained at least four thoracic vertebrae, but proportionately the gain is twice as great in *C. macouni* as in *C. sloani*. This gain is reflected in their generally higher total vertebral counts.

Chauliodus pammelas and *C. schmidt* have a more anteriorly placed dorsal fin than the fossil, but their anal fin placement is the same. *Chauliodus pammelas*, however, shows no increase in thoracic vertebrae and *C. schmidt* only a slight increase.

The number of caudal vertebrae remains essentially the same in all species of *Chauliodus*. This may relate to the fact that ossification is completed first in this region.

Since the number of cervical vertebrae varies directly with the position of the dorsal fin and since the number of caudal vertebrae remains constant, it must be the vertebrae between the dorsal and anal fin that account for the variation in vertebral counts among the species of *Chauliodus*.

Dentition: The significance of the fact that the third premaxillary tooth is longer than the fourth in *C. eximius*, *C. barbatus*, and *C. macouni* may be related to their feeding abilities. It is assumed that those species of *Chauliodus* which retain the acenous cervical vertebrae are able to open their mouths wider because of the increased flexibility of the anterior portion of the vertebral column. *Chauliodus eximius*, *C. barbatus*, and *C. macouni* all have fewer acenous vertebrae as adults than do the other species in the genus. This fact, together with the correlated proportions of the third and fourth teeth, makes it plausible to assume that they cannot open their mouths wide enough for

the fourth tooth to be effective. *Chauliodus sloani*, *C. danae*, *C. pammelas* and *C. schmidtii* retain the acenous condition as an adult and the fourth premaxillary tooth is longer than the third, presumably because it is able to play a greater role in food-getting since the mouth can be opened wider. The fourth premaxillary tooth is shorter in *C. eximius*, *C. macouni*, and *C. barbatus* because an excessively long tooth at that position in the jaw would be ineffective as a food-getting instrument in a fish that cannot open its mouth very wide.

Measurements of length: The position of the dorsal fin suggests that two trends exist in this genus. In one, as exemplified by *Chauliodus barbatus* and *C. danae*, the dorsal fin is moving posteriorly, and in the other, from *C. macouni* to *C. pammelas* to *C. sloani* and *C. schmidtii*, this fin is moving anteriorly. Part of the significance of the dorsal fin position is undoubtedly related to the function of the elongated second dorsal ray. If, as Brandes (1898; cited by Tchernavin, 1953) postulates, this ray bends far forward to dangle a luminous lure to attract prey, then the position of the dorsal fin plus the length of the second ray would play an important role in food getting. Unfortunately, no one has ever seen a living specimen of *Chauliodus* feed. Still another difficulty lies in the fact that this long filamentous ray is quite fragile and is most often broken off during capture. Until sufficient material can be collected to correlate the measurements of the second dorsal ray, this aspect of the problem must lie in abeyance.

Taxonomy: David (1943: 124) suggested that Jordan's specimen of *Chauliodus eximius* from Lompoc, California, might be synonymous with the Southern California subspecies which she named *C. barbatus frazeri*. With more specimens on hand, it became apparent that all the known fossil members of the family Chauliodontidae are indeed the same species. While David's name appropriately connotes a strong resemblance to *C. barbatus*, Jordan's specific name, *eximius*, holds priority and, therefore, must be used to designate the fossil species. Furthermore, since the type specimen of *Chauliodus eximius* has been lost, a specimen from the same formation at Lompoc, California, must be chosen as a neotype. Because the Lompoc specimens are not as clear as those from the Santa Monica Mountains, Los Angeles County, California, a plesiotypic series composed of specimens from this latter locality needs to be established (see below).

Evolution: Morrow (1961) suggests that a *Chauliodus sloani*-like form gave rise to *C. macouni*, *C. danae*, *C. barbatus*, and *C. sloani*. *Chauliodus sloani* then branched off to form *C. pammelas* and *C. schmidtii*. Morrow supports this position by pointing out that a trend exists in the increased number of pigmented SM organs (clusters of minute ventral photophores), in *C. sloani* from the Indo-Pacific area to the Pacific Equatorial water mass with *C. barbatus* as "the end result of whatever forces are at work . . ." (1961: 284). He also notes that the length of the barbel, which is shortest in North Atlantic species, increases in length circum-globally until the greatest length is attained in the mid-Pacific forms.

Until a function is determined for the barbel and the SM organs, it is difficult to assess the significance of their reduction or increase. Presumably structures which confer upon the organism some selective advantage are those which are retained in succeeding generations. Evolutionary trends in this genus cannot be reconstructed reliably on the basis of structures whose functional significance in Recent fish is unknown. Fossil evidence, however, has in this instance provided a structure whose function can be reasonably construed and which is observable in modern members of the genus; that is, the nature of the vertebrae in the cervical region of *Chauliodus*.

It is assumed that any adaptation which would confer greater feeding capability on an organism would give that organism a strong selective advantage over its congeners. Such an adaptation in *Chauliodus* was the indefinite postponement of the ossification of the anterior vertebrae. By being more flexible in the cervical region, those species with this adaptation should be more successful than those retaining the primitive condition. This conjecture is borne out by the observation that those species enjoying the widest distribution are the ones with the acentrous anterior vertebrae; i.e., *Chauliodus sloani* and *C. danae*, while those retaining the anterior ossification characteristic of the fossil species remain relatively restricted; i.e., *C. barbatus* and *C. macouni* (Fig. 12). *Chauliodus pammelas* and *C. schmidtii*, which have very restricted ranges and have acentrous cervical vertebrae, are regarded as recently-evolved species, closely allied to *C. sloani*, whose speciating mechanism probably involved a physical-chemical isolation (see Haffner, 1952).

It does not seem reasonable to argue that an organism would evolve in a direction that would cause it to lose feeding capabilities. This is especially true in a deep sea environment where, presumably, carnivorous fishes compete strongly for food. Within the family Chauliodontidae, therefore, evolution could *only* have progressed in the direction of greater feeding capability, marked by the acquisition of greater flexibility of the neck region.

Evidence supporting the choice of the southern California fossil species as at least part of the ancestral stock for the family is found in two observations. One, the Recent species most closely resembling the fossil form are found in the Eastern Pacific. Two, in other fossil deposits in which the fauna is similar to the southern California fossil fauna, there have been no reports of *Chauliodus*. This is despite the fact that in some instances *C. sloani* is now quite abundant in the waters near these deposits. There is no question regarding recognition of the family in these different deposits since the other bathypelagic fishes therein are beautifully preserved and any such preservation of *Chauliodus* would be instantly identifiable.

If *Chauliodus eximius* formed the primitive stock for the family Chauliodontidae, then the Recent forms morphologically and geographically closest to it should represent the chronologically oldest extant species. These forms are *C. barbatus* and *C. macouni* which still retain the anterior ossification characteristic of *C. eximius* and are found in the Eastern Pacific. Each exhibits the

beginning of two opposite trends in the movement of the dorsal fin relative to its position in *C. eximius*. In *C. barbatus* the dorsal fin is more posterior while in *C. macouni* it is more anterior. Both show a slight increase in the number of cervical vertebrae. As the water temperature in the Eastern Pacific during the late Miocene continued to decrease (Durham, 1960), that portion of the primitive population which was able to adapt to the colder water may have radiated into the North Eastern Pacific waters, increased the number of vertebrae and became *C. macouni*. The remaining part of the population could have contracted southward into the present tropical range of *C. barbatus*.

Following the trend of anterior movement of the dorsal fin, accompanied by a favorable genetic change postponing anterior ossification, *Chauliodus macouni* could have evolved to *C. sloani* in the Western Pacific. Once this highly successful species was established, it probably then invaded the Indo-Pacific area and the Atlantic Ocean. The Peru-Chile Trench population may represent either radiation from the South Atlantic or an eastward migration from the Western Pacific. There appear to be few, if any, barriers to the radiation of this species.

The more posterior position of the dorsal fin in *Chauliodus barbatus* suggests a close relationship to *C. danae*. If the trend to a more posterior placement of the dorsal continued, accompanied by the postponement of cervical ossification, then *C. danae* could quite conceivably have evolved from *C. barbatus*. In this case, however, a geological isolating mechanism is postulated in the form of the closure of the Bolivar Trough sometime in the late Miocene or early Pliocene (Olssen, cited in Whitmore, 1965). If the population of *C. barbatus* once occupied part of the present western Caribbean area and was continuous with the modern tropical Pacific population, it is possible to conjecture that the mutant forms with greater cervical flexion arose in the Caribbean some time near the end of the Miocene. These were cut off from the parent population by the development of the land bridge between North and South America. Their feeding advantage would be great because of lack of cervical ossification in addition to the more posterior placement of the dorsal fin. This species could then radiate throughout the Atlantic and even around to the Eastern Pacific and the Peru-Chile trench.

The apparent overlap in the ranges of *Chauliodus sloani* and *C. danae* could plausibly be explained in terms of varying oxygen concentrations isolating the populations vertically (Haffner, 1952).

An alternative radiation pattern could have been from the Eastern Pacific around South America to the Atlantic. In this case the isolating mechanisms might involve currents and deep trench environments.

The possibility that the fossil, *Chauliodus eximius*, gave rise to *C. sloani* directly by the isolating mechanism postulated for *C. barbatus* to *C. danae*, thus requiring a genetic change for lack of anterior ossification to occur only once, cannot be overlooked. *Chauliodus danae*, *C. schmidtii* and *C. pammelas* would then have evolved from *C. sloani*. The difficulty with this interpretation

is that it requires an anterior movement of the dorsal fin from *C. eximius* to *C. sloani* then back again some 7 per cent of the standard length in order to evolve *C. danae* from *C. sloani*. *Chauliodus danae* is closer to *C. barbatus* in total number of vertebrae, the position of the dorsal fin and the structure of the barbel. It is closer to *C. sloani* in lacking anterior ossification, in having the third premaxillary tooth shorter than the fourth and in general morphometric characters.

Whether *Chauliodus danae* evolved from *C. sloani* or from *C. barbatus* is a problem which, at this point in time, does not seem capable of resolution.

Feeding habits: Eleven specimens of *C. eximius* showed evidence of fossilized fish remains in the area of the stomach (Fig. 13). All such stomach contents showed that *C. eximius* swallowed its prey headfirst. This is consistent with reports of the feeding behavior in the modern members of the genus (Morrow, 1961: 265).

Paleoecology: The punky, white diatomite in which *Chauliodus eximius* occurs forms the major part of the upper strata of the upper Modelo formation interpreted as upper Mohnian and lower Delmontian in age (Hoots, 1931). This late Miocene formation, approximately 15 million years old, is exposed on the northern slopes of the Santa Monica Mountains, Los Angeles County, California. The upper Modelo lies conformably on the lower Modelo which differs in composition because it is composed mainly of hard platy siliceous shales and thinly interbedded sandstone. Megafossils of the upper member are epipelagic and bathypelagic fishes, algal remains, and terrestrial spermatophyte leaves. *Delectopecten pedroanus* Trask is the only mollusk represented. Two crab carapaces and one bryozoan colony have been collected by the author but no report on these has been published. Microfossils other than diatoms include Foraminifera, Radiolaria, sponge spicules, and silicoflagellates.

Hoots (1931: 112) suggested a shallow (95 meters) water origin for at least some of these diatomite deposits. He based his conclusion on the presence of fossil-barren sandstone intercalated with finely laminated diatomaceous shale which, he held, could only have been formed by wave base action. However, it is now thought (Ladd, 1959) that turbidity currents are capable of carrying sand and off-shore terrestrial remains to great depths. David (1943: 79) suggested that the upper Modelo "was laid down in the deep sea but not at a great distance from shore" at depths of 200 to 500 meters in deep basins occurring on the continental shelf or just off the continental shelf. Her conclusions were based on analyses of the fishes present in the faunal assemblage of the upper Modelo of the Santa Monica Mountains. The deep basin interpretation is supported by the physiography of the Recent seascape off the southern California coast (Emery, 1960: 50). Sullwold (1960: 436) suggested, from analysis of the Foraminifera, a depth of 920 meters. Interpretations suggesting depths of 1,000 meters or more are consistent with the depths at which modern species of *Chauliodus* occur.

Determinations of paleotemperature (Emiliani, 1954) indicate that the



Figure 13. Photograph of *Chauliodus eximius* revealing fossilized stomach contents. Note the headfirst position of the ingested fish which is characteristic of the method of feeding in recent *Chauliodus* spp.

climate during the Miocene was warmer than at present. What effect this would have on the bathypelagic environment is uncertain. Since part of the geographic distribution of *Chauliodus* may be related to water temperature (Haffner, 1952), it seems likely that even a small change in the extremes of the temperature range would exert some evolutionary pressure on a bathypelagic genus such as *Chauliodus* which may have influenced its evolutionary pattern.

The preservation of articulated skeletons, the absence of benthonic scavengers, and the evenly layered diatomite suggests a calm sterile bottom similar to present off-shore areas described by Emery (1960: 168): "A parallel effect of low content of oxygen in the water is that much of the organic debris produced near the surface reaches the bottom without having undergone much oxidation during settling; therefore considerable oxidation continues within the bottom sediments . . . the dissolved oxygen . . . becomes depleted" resulting in an inhospitable benthonic environment. This statement also contains a suggestion concerning circumstances that may have originally killed the fishes preserved as fossils. Much work is presently under way on the study of marine sediments which should provide data making interpretation of diatomite deposits more accurate.

DESCRIPTION OF *Chauliodus eximius* (JORDAN AND GILBERT)

Synonymy: *Eostomias eximius* Jordan and Gilbert 1925; Stanford Univ. Press, Univ. Ser: Biol. Sciences, 4:1, p. 13. *Chauliodus barbatus frazeri* David 1943; Geol. Soc. Amer., Spec. Paper 43, p. 61.

Study material: Forty-four specimens, 68 to 161 (200?) mm. standard length. Thirty-three of these are from the upper Modelo formation of the NE slope of the Santa Monica Mountains, Los Angeles County, California (LACM 1267, 1806, 1035, CIT 326). Seven are from Cabrillo Beach, San Pedro, California (LACM 1925). Two are from Sulphur Canyon, Santa Suzanna Mountains, Ventura County, California (CIT 332), and three are from the area near Lompoc, California (LACM 6589, CIT 385).

Type designations: The type of *Chauliodus eximius* (Jordan and Gilbert), originally *Eostomias eximius* Jordan and Gilbert, has been lost. Los Angeles County Museum of Natural History (LACM) specimen No. 11044 from Lompoc, California is hereby designated the neotype. Specimen No. 5253, 11048, 11439, and 11440 from LACM locality No. 1267, specimen No. 5242 from LACM locality No. 1806, and specimen No. 10163 from LACM locality No. 326 (David's type for *C. barbatus frazeri*) are designated plesiotypes.

Diagnosis: General characteristics are those of the family Chauliodontidae. Large fang-like teeth in premaxillary and mandible; elongate body; dorsal fin in anterior one-third with first ray minute, second ray much produced into long filament.

Chauliodus eximius is similar to *C. barbatus* and *C. macouni* in that the third premaxillary tooth is longer than the fourth and ossification proceeds anteriorly up to the first cervical vertebra. *Chauliodus eximius* differs from

these species in proportional distribution of vertebrae, in having fewer cervical vertebrae, in the position of the dorsal fin and in possessing non-recurving teeth. It differs from all other extant species of *Chauliodus* in having ossification of the anterior centra and in not having terminally modified teeth or teeth which recurve.

Description: Proportional measurements given as average percentages of standard length. Range of variation is shown in parenthesis.

Head; 16.8 (15 to 21), N = 14.

Distance from snout; to origin of dorsal fin 26.2 (23.0 to 29.8); to origin of anal fin 85.7 (82.0 to 88.0); to origin of ventral fin 41.4 (37.1 to 45.0), N = 12.

Pre-anal length without head; 68.3 (66 to 72), N = 13.

Origin of dorsal to origin of anal; 59.6 (56.0 to 64.0), N = 13.

Origin of ventral to origin of anal; 44.2 (41.0 to 47.0), N = 14.

Length of caudal peduncle; 6.5 (5.6 to 7.7), N = 14.

Length of mandible; 13.9 (12.6 to 16.3), N = 13.

Dorsal fin; rays 7 to 8 (includes minute first ray), N = 23.

Anal fin; rays 10 to 13, N = 14.

Pectoral fin; length 10.9 (7 to 13.7), N = 12; rays 10 to 13, N = 20.

Ventral fin; length 16.6 (12 to 23.7), N = 10; rays 7 to 8, N = 22.

Vertebrae; (counts exclude first cervical vertebra; see Methods and Materials, above) Total 48?, 50 to 53, N = 15; acenous 1 to 2; most often 1, N = 29; cervical (including acenous vertebrae) 9.2 (8 to 10), N = 22; thoracic 32.1 (30 to 35), N = 12; caudal 9.8 (9 to 11), N = 13.

Serial photophores; Ventral row: VAV 20 or 22, N = 1; PV 17, N = 1. Lateral row present.

Body elongate, slender, depth about 10 per cent of standard length. Barbel not detectable. Head slightly less than 20 per cent of standard length. Orbit not well enough defined to measure.

Mouth large, mandible length about 80 per cent of head. Premaxilla with four teeth, second tooth longest; third longer than fourth (one specimen, third equal to fourth), N = 15. Many small oblique teeth on maxilla. Mandible with up to 7 teeth, generally 6, first tooth about half the length of mandible, longest of any in jaws. Teeth typical of the family Chauliodontidae except that they taper to a point uninterrupted by secondary curving or terminal modifications. Distally the teeth appear translucent and the tip is black. No denticles detectable near corner of mouth.

Dorsal fin with 7 to 8 rays, including minute first ray visible on at least one specimen. Second dorsal ray long, filamentous, at least 33 per cent of standard length. Ventral fin abdominal, length about 15 per cent of standard length with 7 to 8 rays. Pelvic bones elongate, possibly fused anteriorly. Length of pelvic bone 8 (6 to 10) per cent of standard length, N = 8. Anal fin near caudal with 10 to 13 rays. Length of base about equal to pectoral length. Length of caudal peduncle about 7 per cent of standard length.

Size: The largest complete specimen is 161 mm. (LACM 5242) in standard length. The size of the head of an incomplete specimen indicates that *C. eximius* probably grew to at least 200 mm.

Relationships: *Chauliodus eximius* is more closely allied to *C. barbatus* and *C. macouni* than any other extant species. Only these three species share the characteristic of ossified centra in the anterior vertebrae. The third premaxillary tooth is longer than the fourth in all three and in no other members of the family Chauliodontidae. *Chauliodus macouni* and *C. barbatus* are the only Recent species found in the eastern Pacific, which was the habitat of *C. eximius*. It is likely that *C. eximius* was the ancestral stock for both the north temperate *C. macouni* and the tropical *C. barbatus*. Total vertebral count is similar in both *C. eximius* and *C. barbatus* but the distribution of cervical and thoracic vertebrae is different. *Chauliodus macouni* is closer to *C. eximius* in number of cervical vertebrae. Both *C. barbatus* and *C. macouni* differ from *C. eximius* in number of thoracic vertebrae. *Chauliodus eximius* is more distinct from *C. barbatus* and *C. macouni* in number of vertebrae over the pelvic bone than they are from each other. The Miocene species *Chauliodus eximius* is therefore assumed to be the ancestral species which gave rise to *C. barbatus* and *C. macouni*.

CONCLUSIONS

General: The members of the genus *Chauliodus* have not changed in over-all body form since the middle Miocene. Adult specimens of *Chauliodus barbatus* and *C. macouni* have retained the primitive, as defined by the condition in the fossil *C. eximius*, almost completely ossified condition of the anterior vertebrae and also possess the primitive characteristic of having the third premaxillary tooth longer than the fourth. The remaining extant species have developed a tendency to postpone the ossification of the anterior-most vertebrae and have the fourth premaxillary tooth longer than the third.

Vertebral ontogeny proceeded from the caudal region anteriorly in the fossil, *Chauliodus eximius*, as it does in all recent species. Differences in vertebral counts among the various species of *Chauliodus* appear to be attributable to variation in the number of vertebrae in the area between the dorsal fin and the anal fin. The caudal vertebral count is constant for all species, while the cervical vertebral count varies directly with the position of the dorsal in all species except the fossil which has a proportionately lower number of cervical vertebrae.

There is not significant difference in fin ray counts among the various species except for the anal fin in *Chauliodus pammelas* which tends to have two more rays but which is still within the range for the genus.

Evolution: The acquisition of the ability to postpone the ossification of the anterior vertebrae, thus increasing the flexibility of the cervical region and conferring a great feeding advantage, is considered to be the major factor influencing speciation within the genus *Chauliodus* since the middle Miocene.

Because *C. barbatus* and *C. macouni* most closely resemble the fossil *C. eximius* in lacking this ability, they are considered the more primitive recent species. Accepting this, and using as criteria the two trends in the movement of the dorsal fin, i.e., anteriorly versus posteriorly when compared with the fossil, several patterns of radiation are possible. There is not, at this time, sufficient evidence to choose one among them as *the* pattern and therefore, all three are presented. In each case, *C. pammelas* and *C. schmidtii*, because of their great resemblance to *C. sloani* are regarded as species most recently evolved from *C. sloani*. Note that evolution from *C. barbatus* or *C. macouni* requires the selection for postponing time of ossification of anterior vertebrae. Furthermore, it is conceived that *C. sloani* was well established before *C. danae* evolved because of the more wide spread range of *C. sloani*.

1. *Chauliodus eximius* → *C. barbatus* → *C. danae*, which was isolated by the closure of the Bolivar Trough. *Chauliodus danae* then carried throughout the North and South Atlantic, and moved around South America into the Peru-Chile Trench.

Chauliodus eximius → *C. macouni* → *C. sloani* at the extreme Western Pacific range of *C. macouni*. *Chauliodus sloani* then would have radiated westward and into the South Pacific. The westerly movement continued circumglobally until *C. sloani* occupied all oceans.

2. *Chauliodus eximius* → *C. barbatus* → *C. danae* in the southernmost part of the *C. barbatus* range, *C. danae* then radiating from the Peru-Chile Trench into the Atlantic Ocean. The evolution of *C. sloani* would have proceeded as in (1) above.

3. *Chauliodus eximius* → *C. sloani* via either the Bolivar Trough route or around South America. *Chauliodus sloani* would then have evolved *C. danae*, isolation in this case probably being of a physico-chemical nature.

A trend is evident in the modification of the distal portion of the teeth in that the fossil displays a simple curving to the tip, *C. barbatus* and *C. macouni* show a slight recurving, and in the remaining species the teeth tend to expand into a triangular modification as well as being recurved.

Paleoecology: *Chauliodus eximius* probably occupied much the same niche in a Miocene deep basin environment as its related species do today. However, further data on Recent marine sediments are needed to properly estimate the depositional environment of the Modelo diatomite. Records of bottom depth as well as net depth for captures of Recent bathypelagic fishes are needed if an accurate interpretation of the depth of the Modelo basin is to be based on microfossil evidence. The exact vertical position for any species of *Chauliodus* in a specific water mass is presently not determinable from published data.

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Chauliodus eximius: Los Angeles County Museum of Natural History, CIT No. 10163, LACM Nos. 5242 to 5261, 10560, 11038-11044, 11047, 11048, 11228, 11239-11241, 11251, 11440, 11441, 12239, 12410, and three uncatalogued.

Chauliodus barbatus: Scripps Inst. Oceangr., Nos. H52-363 (2), 52-390, H52-404, H52-409, 55-229, 55-244, 55-246, 55-258 (3), 55-265, 60-215, 60-216, 60-232, 60-247, 61-215. University of Southern California, Allan Hancock Foundation, Eltanin Sta. 53, 58 (Peru-Chile Trench).

Chauliodus macouni: Scripps Inst. Oceangr., Nos. 51-363 (9), H5508, H6204 (2), H6204-60.60 (2), H6204-80.55; U.S. Fish Wildl. Serv. Lab., La Jolla, No. 224-1; Univ. So. Calif., Nos. 2943 (4), 7344 (2), 7394, 8020, 8027 (5 postlarval), 8028, 8122, 8236; Univ. Calif. Los Angeles, No. 1036 (cleared specimen); U.S. Fish Wildl. Serv. Lab., Washington, D.C., uncatalogued (3).

Chauliodus sloani: U.S. Fish Wildl. Serv. Lab., Washington, D.C., uncatalogued (20). Univ. of So. Calif., Allan Hancock Foundation, Eltanin 14 (Greenland Cruise), Eltanin 743 (2) (Peru-Chile Trench). Scripps Inst. Oceanography, La Jolla, Calif.: SIO 65-621 (1).

Chauliodus danae: Mus. Comp. Zool., Harvard Univ., Nos. 42247 (2), 42249 (8); Univ. So. Calif., Allan Hancock Foundation, Eltanin 52, 61, 165, 741, 742 (2) (Peru-Chile Trench).

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ADDENDUM

After this paper was in galley proof, a juvenile *Chauliodus eximius*, 50 mm. in standard length, was collected by John E. Fitch at Lompoc, California. The specimen, LACM 17143, shows weak anterior ossification. The number of vertebrae in this region is not determinable.